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NOTES ON THE MOTH *PERICOPUS LEUCOPHAEA* WALKER (LEPIDOPTERA: PERICOPIDAE) AS A DEFOLIATOR OF THE TREE *VERNONIA PATENS* H.B.K. (COMPOSITAE) IN NORTHEASTERN COSTA RICA

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Abstract.—Two closely-spaced individuals of the woody composite *Vernonia patens* H.B.K. were severely defoliated by the brightly-colored, gregarious larvae of the moth *Pericopus leucophaea* Walker (Lepidoptera: Pericopidae) in northeastern Costa Rica. Although many other individuals were examined, no other *V. patens* were found to be defoliated. A group of 66 larvae was found on the larger tree and 20 on the smaller one. At the beginning of a three-day period of observation, about 70% of the larger tree and 40% of the smaller tree was defoliated. Defoliation apparently begins on the lower leaves and spreads towards the top. No larvae disappeared during the study period, suggesting high survivorship. Although individuals of the social paper wasp *Polybia simillima* Smith (Hymenoptera: Vespidae: Polistinae: Polybiini) made repeated attempts to capture larvae, all were unsuccessful. When disturbed by wasps, larvae drop from the plant, either suspending themselves on silken threads or falling into the dense undercover. Larvae thus dislodged successfully relocate the plant as they are capable of very rapid locomotion. When prodded with forceps, larvae exhibit strong thrashing movements and exude droplets of a clear fluid which may have a defensive function. Both the aposematic appearance and behavior of the larvae (and adults) suggest unpalatability. Unusually attractive conditions of individual plants, and high survival of egg masses and larvae, probably promote defoliation. Various factors are predicted to determine intensity of defoliation and comprise a basis for further study of this interesting system.

Vernonia patens H.B.K. is a locally abundant woody composite of secondary-growth habitats in the premontane and lowland tropical wet forest regions of northeastern Costa Rica. This small tree (canopy about 4–5 meters tall) of woody shrub often grows as small clumps or single individuals in regenerating fields and along the edges of forest, habitats where it is used as a feeding and chorusing site for various species of cicadas (Homoptera: Cicadidae) (Young 1980a, b). The purpose of this brief communique is to report the severe defoliation of two individuals of this tree species by the gregarious larvae of the medium-sized (i.e. wingspan of 40 mm) moth *Pericopus leucophaea* Walker (Lepidoptera: Pericopidae) in this region of Costa

Fig. 1. The larger of the two *Vernonia patens* (Compositae) defoliated by the gregarious larvae of the moth *Pericopus leucophaea* (Lepidoptera: Pericopidae) at one site in northeastern Costa Rica, February 1981. Note the severe defoliation of the lower branches of this tree and the relatively intact crown of young leaves. When disturbed by *Polybia* wasps the aposematically-colored larvae drop off the tree into the dense ground cover below, and then crawl back to the same plant.

Rica during the dry season. The general pattern of defoliation of the two trees, and the ineffectiveness of a social paper wasp, *Polybia simillima* Smith (Hymenoptera: Vespidae: Polistinae: Polybiini) as a predator on the larvae of this species, are described for the first time.

Methods

On 3 February 1981, I discovered two closely-spaced *Vernonia patens* trees, one about 1.5 meters tall and the other about 2.5 meters, in different stages of noticeable defoliation by the gregarious larvae of an unidentified moth species. The location of these trees, about 3 meters apart, is along a gravel road at "Finca La Tigra," near La Virgen (10°23'N, 84°07'W; 220 m. elev.), Heredia Province, Costa Rica. The habitat is a road-side patch of regenerating secondary vegetation, and no other individuals of *V. patens* were found within 20 meters in any direction from this "island." Between 3 and 5 February, I made daily observations on the number of larvae present, their behavior, the amount of defoliation of each tree, and the interaction of the larvae with other arthropods. I checked the two trees at various times each day, to determine larval feeding patterns, if any, and changes in the location of larvae on the trees. A sample of 20 larvae was collected the evening of 5 February and confined, along with fresh cuttings of the food plant, to a clean, clear-plastic bag, for rearing to the adult stage since I had to leave the site at this time. The captured larvae were taken to other sites in Costa Rica, until 25 February, at which time they were taken to Milwaukee, Wisconsin (as pupae) to complete the rearing.

At several times during the field study, the larvae were prodded with forceps to elicit defensive behavior.

Results

At the time of discovery, approximately 70% of the leaves from the larger of the two trees had been stripped from the trees (Fig. 1), and about 40% of the leaves of the smaller tree were gone. That the leaves had been eaten by the larvae was verified by examining the number of chewed petioles, and distinguishing these from regular leaf-drop.

Based on voucher specimens of larvae, pupae, and adults, the moth was identified later as *P. leucophaea*. No other lepidopterous larvae were found on the trees, and with the exception of an occasional orthopteran, no other herbivorous insects were found during daytime hours. A brief inspection of an additional 20 individuals of *V. patens* of similar size, scattered over the site, failed to turn up additional larvae of *P. leucophaea*. At the time of discovery the larvae were easy to spot from a distance of about 5 meters with unobstructed view from the road, owing to their bright color patchwork

Fig. 2. Gregarious behavior and defoliation by larval *Pericopus leucophaea*. Left: cluster of larvae, forming a conspicuous mass (to the human observer) amidst the defoliated branches of the food plant and just below the crown. Right: the larvae form tightly-packed aggregations on branches, petioles, and leaf midribs, bared by defoliation.

of red, white and black, and their gregarious habit (Fig. 2). At this time the larvae were about 15 mm long. During the three days of observation, there were 66 larvae on the larger tree, and 20 on the smaller tree.

Larvae feed intermittently throughout the day, but become very quiescent by 5:30 p.m. As many as ten *Ectatomma* ants were seen crawling over the leaves of each tree during this study, sometimes on the same leaves where larvae were resting or feeding. The ants did not attack the larvae. Defoliation apparently started near the bottom of the tree since the crown of each tree was largely intact (Fig. 1), and most of the *Ectatomma* were found on these young leaves.

Tight clusters of larvae were seen on defoliated petioles and leaf midribs (Fig. 2), rendering them very conspicuous to the human eye. When resting in clusters (Fig. 2), individual larvae, when gently poked with a forceps, exhibit rapid thrashing movements of the anterior half of the body, and produce small clear droplets, which were first noticeable on some of the

Fig. 3. Gregarious feeding and defensive behavior by the larvae of *Pericopus leucophaea*. Top: a typical larval aggregation on the underside of a mature leaf of *Vernonia patens*. The light areas on the bodies of the larvae are bands of white and orange interspersed with bands of black. Below, left: gregarious feeding. Below, right: the larva in full view at the top has just exuded a large droplet of clear fluid on the dorsal bristles just before the posteriorly-terminal segments. This fluid may have a defensive function.

long hairs of body segments (Fig. 2). Sometimes clusters of many larvae were seen on the undersides of leaves, and such leaves were usually quickly defoliated (Fig. 3). The positions of groups varied greatly each day, presumably as a result of feeding activity. Sometimes there were both solitary larvae and several small clusters (Fig. 3) on the larger tree.

On 4 February, I observed from 1 to 3 individuals of the polybiine wasp *Polybia simillima* make repeated attempts to capture larvae, either ones in clusters or single individuals. From a total of 45 predatory-attack attempts observed, none was successful. On a typical attack, a wasp would weave among the leaves and upon discovering one with larvae on it, it would then land on the dorsal side of the leaf, crawl a bit, and then quickly flip over to the ventral side to capture a larva. But at the moment the wasp landed, most of the larvae dropped off the leaf, some suspended on long silken threads, while others (most) fell into the dense herbaceous layer beneath the tree. For a total of twelve larvae followed after falling into the dense cover on different occasions, each one returned to the food plant. The larvae crawl very rapidly when disturbed, and one dislodged from the food plant is usually back on it within five minutes after a fall. Larvae suspended on threads usually dropped to the ground and then crawled to the food plant.

Deliberate mechanical disturbance of larvae on leaves with forceps does not elicit the "dropping off" behavior. In the larger group of larvae, there were two sized classes apparent, the larger sub-group of 45 individuals being about 15 mm long, and the smaller ones, about 10 mm long. All individuals in the group of twenty on the smaller tree were the same size (20 mm long).

In captivity, larvae pupated about 18 days after discovery, each one forming a loose cocoon wrapped in a leaf. The pupa stage lasted about 18 days in this study.

By the end of the field study, both trees were almost entirely defoliated, save for small crown areas of young leaves on each one. Since it required more than two additional weeks to bring larvae to pupation, both trees would have been insufficient total food supply for the larvae under natural conditions.

Discussion

The defoliation of individual food plants by a herbivorous insect species in the tropics may be considered an "outbreak" if a large portion of the local food plant population is defoliated. The defoliation of a few individuals of such a population, however, may be a result of isolated patches where survival of the herbivore is unusually high, and may not necessarily be an "outbreak." A variety of ecological factors, including the degree to which

patches of varying size of a plant species experience severe defoliation, determine pest outbreak conditions in the tropics (e.g., Rey et al. 1981).

While the present study on the interaction of *P. leucophaea* with *V. patens* is very preliminary, the data suggest that defoliation of a few closely spaced individuals of the food plant resulted from an "escape" of a few egg clusters of the moth from regulatory agents such as predators and parasitoids. There is, however, a growing body of evidence showing that the early stages of Lepidoptera are sources of prey for a variety of arthropods (e.g., Gilbert and Singer 1975).

There have been very few studies of pericopid moths anywhere, save for some systematic and survey studies (e.g., Kendall 1970, 1974; Beutelspacher 1976) and very little is known about the food plant associations of individual species within and outside of the tropics. Presumably the moth places large egg clusters on the food plant, and upon hatching, the larvae exhibit pronounced gregariousness as shown in the present study. Studies of noctuid and arctiid moths feeding on *Vernonia* species indicate considerable food plant specificity in terms of species exploited (e.g., Tietz 1951; Burnett et. al. 1974). To the human observer, the brightly-colored larvae of *P. leucophaea* and their gregarious behavior on the food plant suggest aposematic display and unpalatability. Some *Vernonia* contain high concentrations of bitter sesquiterpene lactones in the leaves (Abdel-Baset et al. 1971; Mabry et al. 1975), which could be the basis for suspected unpalatability of some herbivores such as *P. leucophaea* if these compounds are incorporated into the insects. These compounds have also been demonstrated to be a basis for oviposition preferences in various Lepidoptera exploiting some species of *Vernonia* (Burnett and Jones 1978).

Because sesquiterpene lactones in some *Vernonia* have been shown to deter feeding by some Lepidoptera (Burnett et al. 1974), the aposematic coloration of both the larvae and adult stages of *P. leucophaea* may be indirect evidence that this species is able to sequester and incorporate these compounds. Relative to what is known about the feeding-deterring properties of these compounds for other Lepidoptera (Burnett et al. 1974), and assuming these compounds to be present in the age-classes of leaves of *V. patens* exploited by larval *P. leucophaea,* this moth may have entered into a new adaptive zone (in the context of Ehrlich and Raven 1965). The vivid color pattern of the adult moths, with wings banded in black, white, and red, not only suggests unpalatability, but also mimetic resemblance to female *Parides* (Lepidoptera: Papilionidae: Papilioninae: Troidiini) found in the same habitats (e.g., *P. iphidamas*—see Young 1977b). Adult *P. leucophaea* fly during the daytime and could possibly participate in a Mullerian mimicry association with these Aristolochia-feeding butterflies, even though the moths are somewhat smaller than typical female *Parides*.

The association of *P. leucophaea* with *V. patens* in Costa Rica may be a very specific interaction. It would be expected that a group-feeding brightly-colored herbivore such as *P. leucophaea* would have evolved effective defense mechanisms against predators and parasitoids. My preliminary observations on the ineffectiveness of the wasp *P. simillima* to successfully capture the larvae supports the contention of effective defenses being operative. Thus, in addition to the suspected systemic unpalatability, the composition and functional role of the observed droplets of fluid exuded by the larvae when prodded warrants further study in this context.

A plausible working hypothesis for detailed study of the *P. leucophaea* × *V. patens* interaction in Costa Rica may be that individual egg masses, if escaping from predation or parasitism, result in large groups of larvae which generally have high survival on the food plant. Although *Polybia* wasps at this locality are successful at capturing the gregarious larvae of the butterfly *Mechanitis isthmia* Bates (Lepidoptera: Ithomiidae) on *Solanum* spp. (Solanaceae) (Young 1978), presumably the larvae of *P. leucophaea,* although also gregarious, have an effective means of making *Polybia* attacks very unsuccessful, if my observations are representative of such interactions. In the *Mechanitis* study, *Ectatomma* was also present in close proximity to the larvae, and neither attacked the larvae nor provided an effective defense against the *Polybia* attacks. In the present study, the effectiveness of *P. leucophaea* larvae in escaping from *Polybia* attacks appears to be intrinsic to the larvae, with *Ectatomma* having no apparent effects on the interaction.

When egg and larval survival is high, defoliation of individual food plants may occur. The severity of such defoliation will be a function of the effective size of the egg masses on each individual plant (i.e., the number of eggs hatching) and the physiological receptivity of the individual plant to the larvae. As shown by my preliminary data, smaller numbers of larvae on a plant result in less damage than larger numbers on a larger plant. For *P. leucophaea,* egg masses are presumably placed on lower leaves since the defoliation begins at the bottom of the plant and spreads upwards. As my observations were made in the short and erratic dry season of this region, the possibility exists that conditions resulting in localized defoliation of *V. patens* may be seasonal.

The ability of the larvae of *P. leucophaea* to crawl very rapidly may allow them to encounter other individuals of the food plant when defoliation is severe.

Under conditions of relaxed predation or parasitism on eggs and larvae, one consequence of massive group-feeding is the rapid defoliation of the food plant. Enforced emigration to fresh plants, made possible by high locomotory ability, allows the larval population to re-distribute on the food plant population.

Since *V. patens* often occurs in clumps of varying sizes abundant over relatively small areas of habitat, when conditions are favorable for the survival of large numbers of eggs and larvae, larval dispersal behavior and successful encounter of fresh food plants may prevent localized extinctions.

In the tropics in particular, defoliation by herbivorous insects should be considered as highly transient and ephemeral conditions associated with changes in food plant distribution, community structure, and kinds of control mechanisms operative on populations (e.g., Rey et al. 1981). The degree to which an individual of *V. patens* will be defoliated by *P. leucophaea* is therefore directly related to a wide variety of factors, including (a) attractiveness of the individual for oviposition by the moth and numbers of egg masses deposited, (b) survival patterns of eggs and larvae, (c) effects of other herbivores on this *individual* plant, (d) the dispersal strategy of mated female moths, (e) the degree of oviposition preference for *V. patens,* and (f) the effects of seasonality on (a–e), if any. A complete understanding of severe defoliation of plants other than crops in the tropics requires a consideration of these factors. Such factors determine the carrying capacity of the environment at any one point in time for herbivores such as *P. leucophaea* on *V. patens.*

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